

Eating behaviours in healthy young adult twin pairs discordant for body mass index

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1. Abstract

We aimed to study which eating behavioural traits associate with body mass index (BMI) among BMI-discordant twin pairs. This cross-sectional study examined self-reported eating behaviours in 134 healthy young adult twin pairs (57 monozygotic [MZ] and 77 same-sex dizygotic [DZ]), of whom 29 MZ and 46 DZ pairs were BMI-discordant (BMI difference $\geq 3 \text{ kg/m}^2$). In both MZ and DZ BMI-discordant pairs, the heavier co-twins reported being less capable of regulating their food intake optimally than their leaner co-twins, mainly due to “frequent overeating”. Furthermore, the heavier co-twins reported augmented “disinhibited eating”, “binge-eating scores” and “body dissatisfaction”. The twins agreed more frequently that the heavier co-twins (rather than the leaner co-twins) ate more food in general, and more fatty food in particular. No significant behavioural differences emerged in BMI-concordant twin pairs. Overeating – measured by “frequent overeating”, “disinhibited eating”, and “binge-eating score” – was the main behavioural trait associated with higher BMI, independent of genotype and shared environment.

Keywords: Twins, body mass index, obesity, eating behaviour, disinhibition, overeating

Eating behaviours involve dietary and psychological traits in regulation of food intake and weight management. Eating behaviours vary strongly between individuals, and are regulated by complex interactions between physiological, psychological, environmental, and genetic factors (Grimm & Steinle, 2011). Obesity is considered to be primarily caused by overconsumption (Swinburn, Sacks, & Ravussin, 2009), which is a plausible consequence of disrupted eating behavioural traits (Bryant, King, & Blundell, 2007; Bublitz, Peracchio, & Block, 2010; van Strien, Herman, & Verheijden, 2012). Although subjects with obesity seldom self-report higher energy intake than do those at a healthy weight (Goris, Westerterp-Plantenga, & Westerterp, 2000; Pietiläinen et al., 2010), obesity and increased body mass index (BMI) have, in questionnaires on eating behavioural patterns, been consistently associated with disinhibition of eating (Bryant et al., 2007).

The disinhibited eating measure encompasses social, taste, and emotional triggers for overeating (Hyland, Irvine, Thacker, Dann, & Dennis, 1989). Emotional eating (as a result from negative emotions) and external eating (vulnerability to tempting food signals) may moderate the relationship between overeating and weight increase in adults (van Strien et al., 2012). Perhaps as a consequence of weight gain, individuals with obesity are often dissatisfied with their bodies (Weinberger, Kersting, Riedel-Heller, & Luck-Sikorski, 2016), which in turn may be one motivation to lose weight (Vartanian, Wharton, & Green, 2012). A common weight-loss approach is dietary restraint; a cognitive effort to self-restrain caloric intake (Lowe, Whitlow, & Bellwoar, 1991). Its relationship with BMI is complex and ambiguous. Dietary restraint seems to be necessary for the treatment of obesity through energy restriction, though it may increase risk for eating pathology and obesity if practiced inappropriately (Schaumberg, Anderson, Anderson, Reilly, & Gorrell, 2016).

When investigating predictors of obesity, it is relevant to control for genetic factors. Currently over 500 genetic loci related to adiposity traits have emerged through genome-wide association studies (Loos, 2018), and many of these loci are also associated with eating behaviours (Grimm & Steinle, 2011).

One can control for genetic factors through the phenotype-discordant monozygotic (MZ) twin pair method (Vitaro, Brendgen, & Arseneault, 2009), a unique example of a case-control study wherein participants are fully matched for genotype, sex, age, and shared environmental factors, but vary in a particular variable such as BMI. Any behavioural differences within MZ twin pairs are plausibly due to environmental experiences and exposures that are unique to one of the twins in that pair. In dizygotic (DZ) twin pairs, behavioural differences result from both environmental and genetic differences, because they share approximately 50% of their segregating genes.

Studies employing an obesity-discordant MZ twin design with twins rating their eating behaviours in relation to their co-twin's (Pietiläinen et al., 2010; Rissanen et al., 2002), have revealed that most twin pairs agree that the co-twins with obesity eat more food overall (Pietiläinen et al., 2010; Rissanen et al., 2002), prefer fatty food (Rissanen et al., 2002), and consume less healthy food (Pietiläinen et al., 2010). This implies that these behaviours are associated with acquired obesity. In another study, including both MZ and DZ twins, ingestion of more food in general was the strongest independent correlate of intra-pair BMI differences (Bogl, Pietiläinen, Rissanen, & Kaprio, 2009).

Overall, most studies have only investigated a limited number of eating behavioural traits in relation to obesity in the same population, and therefore lack a more global view on the patterns behind weight control (French, Epstein, Jeffery,

Blundell, & Wardle, 2012). Several studies have also been unable to control for any genetic influences on the association between eating behaviours and obesity. Building upon current knowledge of eating behaviours and obesity by assessing a wide variety of eating behavioural traits within healthy young adult BMI-discordant MZ and DZ twin pairs, we attempted to uncover which eating behavioural traits are associated with BMI independent of genetic background and of shared environmental factors.

2. Materials and Methods

2.1 Participants

This cross-sectional study included 134 young adult twin pairs (57 MZ and 77 same-sex DZ twin pairs, aged 22 to 36), of whom 29 MZ and 46 DZ pairs were BMI-discordant (BMI difference ≥ 3 kg/m²). The cut-off point for BMI-discordance was defined earlier (Hakala, Rissanen, Koskenvuo, Kaprio, & Rönnekaa, 1999; Rönnekaa et al., 1997). The remaining 28 MZ and 31 DZ BMI-concordant twin pairs (BMI difference < 3 kg/m²) functioned as reference groups to compare eating behaviours when BMI within the twin pairs was similar. Recruitment was from two population-based longitudinal studies of ten complete Finnish birth cohorts from 1975-1979 and 1983-1987 (FinnTwin12 and FinnTwin16, n=5,417 pairs) (Kaprio, 2013), with data retrieved between 2003 and 2013. We took advantage of all the follow-up time points after age 20 from wave 4 in FinnTwin12 (mean age 22 years) and both waves 4 and 5 follow-ups in FinnTwin16 (i.e. ages 25 and 35 years) to find the rare BMI-discordant MZ twins. If the twin pair had attended twice, the latter year was selected. For the DZ twins, we only studied BMI-discordant pairs from the 25-year follow-up of the FinnTwin 16 because at that age a sufficiently large group was

achieved. Additionally, a statistician created an algorithm to randomly select BMI-concordant twin pairs to approximately match the number of discordant twin pairs. Participants were enrolled based on their responses to questions on height and weight at a young adult age, with the aim to cover the full BMI range of subjects with healthy weight and with obesity, and a wide range of intra-pair BMI differences. One exclusion criterion for all twins was clinical diagnosis of an eating disorder, or any mental or medical disease, in order to investigate common variations in eating behavioural traits, not those induced by disease or disorder. Informed consent came from all individual participants included in the study. The study was approved by the Ethics Committee of Helsinki University Central Hospital.

2.2 Anthropometric measurement

Height and weight were measured objectively to calculate BMI. Fat mass and body fat percentage were assessed with dual energy x-ray absorptiometry (DEXA). Zygosity of the twin pairs was confirmed through genotyping of multiple genetic markers from large genotyping arrays with hundreds of thousands of genetic variants (Illumina 670 & Illumina Human CoreExome chips). More details on anthropometric assessment methods can be found in (Jukarainen et al., 2016).

2.3 Food diary

To create a basic dietary profile, the participants kept a 3-day food diary (two working days and one non-working day). A registered dietician provided instructions for the dietary-intake recording, using the program Diet32 (nowadays AivoDiet) to calculate food consumption and energy intake (Mashie FoodTech Solutions AB, 2017); this is

based on 'Fineli'; the Finnish National Food Composition Database (Finnish food composition database., 2009).

2.4 Food intake regulation

The twins selected one from four statements about their to ability to regulate food intake (Supplementary Text S1), as in earlier studies (A. Keski-Rahkonen et al., 2007; Anna Keski-Rahkonen et al., 2005; Pietiläinen et al., 2010): Shortened descriptions of the answer categories were “1. Optimal eating, 2. Frequent overeating, 3. Frequent restricted eating, and 4. Alternating overeating and restriction”. However, due to sparse data for some uncommon behaviours, we collapsed categories 2, 3, and 4 into one category for data analysis, creating a single variable with two values: “non-optimal eating” versus “optimal eating”.

2.5 Eating behaviour

Four eating behaviour questionnaires were used in this study. The Three Factor Eating Questionnaire (TFEQ), to investigate cognitive restraint of eating, disinhibited eating, and susceptibility to hunger (Stunkard & Messick, 1985). These TFEQ outcome measures were further divided into seven subscales: flexible control (gradual and subtle approach of limiting food intake) and rigid control (all-or-nothing approach) (Westenhoefer, 1991); habitual, emotional, and situational susceptibility to disinhibition (Bond, McDowell, & Wilkinson, 2001); and internal locus for hunger (regulated and interpreted internally) and external locus for hunger (triggered by external cues) (Bond et al., 2001). The Dutch Eating Behaviour Questionnaire (DEBQ) comprises emotional eating, external eating, and restrained eating (van Strien, Frijters, Bergers, & Defares, 1986). The Binge-eating Scale (BES) assessed

the severity of and preoccupation with binge eating (Gormally, Black, Daston, & Rardin, 1982). Three variables from the Eating Disorder Inventory-2 (EDI-2) included were drive for thinness, body dissatisfaction, and bulimia (Garner, 1991).

The DEBQ, TFEQ, and EDI-3 (similar to EDI-2) are valid and reliable measures for individuals with overweight and obesity when compared to leaner controls (Bohrer, Forbush, & Hunt, 2015). BES is a valid and reliable measure for both objective and subjective binge-eating severity (Timmerman, 1999).

2.6 Co-twin comparison questionnaire

Co-twins rated each other's eating behaviours in the previous 12 months through a questionnaire that inquired about ten dietary intake and related behavioural aspects, answering "which of you (you or your co-twin)...", for example, "...eats more?, ...eats more fatty foods?, ...eats more slowly?" (Supplementary Text S2), see also (Bogl et al., 2009).

2.7 Data analysis

Stata/SE 13.0 (StataCorp, College Station, TX) served for statistical analyses. Non-parametric statistical tests were performed because of small sample size and non-normal distribution of the majority of the data. All statistical tests we performed, unless stated otherwise, within BMI-discordant and -concordant MZ and DZ twin pairs separately. The cut-off point to indicate statistical significance was $p < 0.05$. Since not all questionnaire data was complete, a table of the number of twin pairs who completed each questionnaire is in the supplementary material (Supplementary Table S1), which is available on the Cambridge Core website.

2.7.1 Anthropometry and food diary

Intra-pair differences in the anthropometric measures were examined with Wilcoxon signed-rank tests, and this test also compared dietary intake and macronutrient proportion in the leaner versus heavier co-twins. Anthropometry measures were compared between leaner MZ and DZ co-twins, and heavier MZ and DZ co-twins with Mann-Whitney U tests. Calorie intake and relative consumption of macronutrients (fat, protein, carbohydrates, and alcohol) in grams per day, and in percentages of energy intake, were calculated according to Fineli (the Finnish food composition database. 2009). All other dietary components appeared as grams consumed per day.

2.7.2 Food intake regulation

The prevalence of optimal eating and non-optimal eating between leaner and heavier co-twins was examined by McNemar's test. Prevalence of optimal and non-optimal eating was reported, as well as absolute prevalence differences.

2.7.3 Eating behaviours

Scores on the separate domains of the TFEQ, DEBQ, BES, and EDI-2 were adjusted to a scale of 0-100 for easier interpretation and comparison (Lauzon et al., 2004), which means that the lowest possible score was subtracted from the actual score and divided by the possible score range, multiplied by 100 (Lauzon et al., 2004). For example, suppose the total score ranges from 12 to 40. If someone scored 26, then the calculation would be $(26 \text{ (actual score)} - 12 \text{ (lowest score possible)}) \div (40 - 12 \text{ (score range)}) \times 100 = 50$. The original cut-off points for interpretation of the BES score were "severe binge-eating if BES score ≥ 27 , moderate bingeing, 18-26, and

no bingeing, ≤ 17 " [24]. The new scale of 0-100 gave as cut-off points "severe binge-eating if BES score ≥ 59 , moderate bingeing, 38-58, and no bingeing, ≤ 37 ". The other questionnaires were evaluated as higher score reflecting more extreme behaviour.

First, survey regression analyses assessed coefficients for the association between standardized behavioural traits (i.e. divided by standard deviation) and BMI as a continuous variable in all twin individuals. A correction was applied for the familial grouping of traits, with age and sex included as covariates. BMI, because of its intuitive interpretation, was not standardized. Behaviour standardization enabled equal comparison between associations with BMI.

Subsequently, we analyzed the differences in responses on the TFEQ, DEBQ, BES, and EDI-2 questionnaires between leaner and heavier co-twins with Wilcoxon signed-rank tests. We quantified the size of the significant differences with the common language effect size (McGraw & Wong, 1992). This effect size identifies those cases in which the heavier co-twin scores higher on a behavioural trait than does the leaner co-twin as a proportion of the total twin pairs. Thus, put simply: an effect size of 0.68 for emotional eating signifies that the chance is 68% that in any random twin pair, the heavier co-twin experiences higher level of emotional eating. Importantly, an effect size of 0.50 implies that any difference between co-twins is due solely to chance. Hence, an effect size above 0.50 implies a probability superior to chance that the heavier co-twin performs a behavioural trait more strongly, whereas below 0.50, the heavier co-twin is less likely to do so. We calculated approximate confidence intervals (CI) for effect sizes, as discussed in more detail elsewhere (Altman & Bland, 2011).

239 Additionally, we created a correlation matrix of all eating behavioural traits –
240 with a correction for familial clustering – to obtain a better understanding of the
241 overlap or similarity between traits.

243 *2.7.4 Co-twin comparison questionnaire*

244 The co-twin comparison questionnaire we analyzed separately for MZ and DZ twins –
245 but we combined BMI-discordant and -concordant twins – in two ways: with Wilcoxon
246 signed-rank tests and multivariate regression analyses, as earlier (Bogl et al., 2009).

247 Only those twin pairs who provided internally consistent answers as to who
248 performed a particular eating behaviour more strongly we included in the Wilcoxon
249 signed-rank tests. The twin pairs were separated into Twin1 (who performed the
250 behaviour more strongly according to both co-twins of the pair), and Twin2 (who
251 performed the behaviour to a lesser extent). Wilcoxon signed-rank tests compared
252 the differences between the average BMI of Twin1 and Twin2, for all eating
253 behavioural traits, providing the mean difference in BMI (kg/m^2) for each eating
254 behavioural trait.

255 Multivariate regression analyses were performed in all twin pairs. A twin pair
256 was coded -1 if both co-twins agreed that the leaner co-twin performed the
257 behaviour, +1 if both agreed the heavier co-twin performed the behaviour, and 0 in all
258 other cases. This allowed linkage of independent eating behavioural to intra-pair
259 differences in BMI (BMI heavier co-twin - BMI leaner co-twin), while controlling for
260 age and sex.

3. Results

3.1 Characteristics and dietary profile in leaner versus heavier co-twins

All adiposity measures were higher in the heavier co-twins of MZ and DZ pairs discordant for BMI (Table 1), as expected with this study design. The leaner co-twins of the MZ twins were on average in the overweight category, and the heavier co-twins in the obesity class I category. In the DZ twin pairs, the leaner co-twins on average were of a healthy weight and the heavier co-twins had overweight. Moreover, in the BMI-concordant twins, small intra-pair differences in adiposity were evident, because of the division into leaner and heavier co-twins (Supplementary Table S2). An overview of all BMI category (e.g. overweight, obesity class I) comparisons in the whole cohort, and separately by zygosity and BMI-discordance is available (Supplementary Table S3).

In BMI-discordant twin pairs, both leaner and heavier MZ co-twins had a higher age, BMI, fat mass, and fat percentage than the leaner and heavier DZ co-twins (Supplementary Table S4), and higher weight in leaner MZ co-twins only. Sex and height followed similar patterns between MZ and DZ co-twins. No evidence was present for any difference in BMI-concordant twin pairs between leaner MZ and DZ co-twins or heavier MZ and DZ co-twins.

The food diaries did not reveal any meaningful differences in caloric intake or relative intake of macronutrients between leaner and heavier co-twins in any of the groups (Supplementary Table S5).

Table 1: Intra-pair differences in characteristics of MZ and DZ twin pairs discordant for BMI.

	BMI-discordant twin pairs							
	MZ (n=29)				DZ (n=46)			
	Leaner	Heavier	$\Delta\%$	p-value	Leaner	Heavier	$\Delta\%$	p-value
Age, y	30.1 \pm 0.9	30.0 \pm 0.9	-	-	27.4 \pm 0.3	27.5 \pm 0.3	-	-
Female/male, freq.	19/10	19/10	-	-	21/25	21/25	-	-
Height, cm	172.6 \pm 2.1	172.9 \pm 2.0	0.2	0.52	173.3 \pm 1.2	174.8 \pm 1.3	0.9	0.12
Weight, kg	76.6 \pm 3.4	94.9 \pm 3.9	23.9	<0.001	65.0 \pm 1.4	87.6 \pm 1.9	35.0	<0.001
BMI, kg/m ²	25.6 \pm 1.0	31.6 \pm 1.1	23.4	<0.001	21.5 \pm 0.4	28.7 \pm 0.6	33.5	<0.001
Fat mass, kg	25.6 \pm 2.2	39.3 \pm 2.2	53.5	<0.001	14.8 \pm 1.2	31.1 \pm 1.7	110.1	<0.001
Body fat, %	32.3 \pm 1.9	41.4 \pm 1.4	28.2	<0.001	22.3 \pm 1.6	35.2 \pm 1.6	57.8	<0.001

Values are mean \pm standard error. BMI=body mass index, MZ=monozygotic, n=number of pairs, DZ=dizygotic, $\Delta\%$ =difference in percentages [(heavier-leaner)/leaner \times 100], freq.=frequency.

3.2 Food intake regulation in leaner versus heavier co-twins

In MZ and DZ BMI-discordant twin pairs, McNemar's test indicated that regarding food intake regulation, leaner and heavier co-twins differed (MZ: $\chi^2=7.36$, $p=0.01$; DZ: $\chi^2=9.31$, $p=0.003$; Figure 1). The non-optimal eating prevalence in leaner versus heavier co-twins was 52% versus 83% in MZ pairs, and 29% versus 60% in DZ pairs. Thus, in both MZ and DZ pairs, the absolute prevalence of non-optimal eating was 31% higher in the heavier co-twins. Less than half of the leaner MZ (48%), but the majority of leaner DZ (71%) co-twins ate optimally. The majority of the heavier co-twins in the MZ (59%) and DZ (51%) BMI-discordant groups frequently overate. Only a few individuals in all groups frequently restricted their food intake (3–13%). In the BMI-concordant groups, leaner and heavier co-twins (58–71%) mainly ate optimally (Supplementary Figure S1), and thus did not differ in food intake regulation.

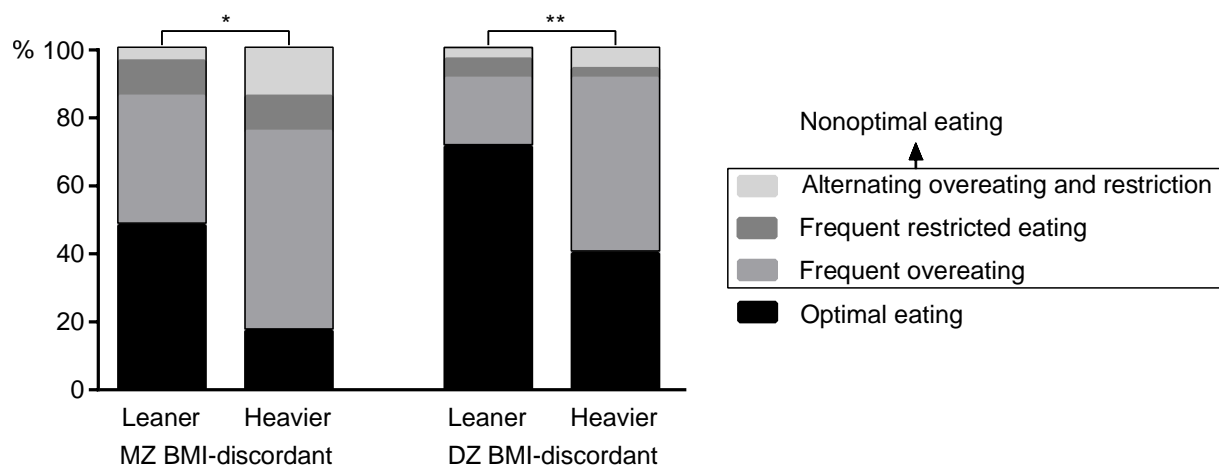


Figure 1: Percentages of food intake regulation categories in leaner and heavier monozygotic (MZ) and dizygotic (DZ) twins discordant for body mass index (BMI). McNemar's test * $p < 0.05$, ** $p < 0.01$.

3.3 Eating behaviours in leaner versus heavier co-twins

P-values from survey regression analyses in all twin individuals demonstrated strong evidence for the presence of associations of standardized disinhibited eating, restrained eating, binge-eating score, drive for thinness, body dissatisfaction, and bulimia with BMI as a continuous variable (Table 2).

308 Table 2: Survey regression coefficients of the association between standardized eating behavioural
309 traits and BMI as a continuous variable

BMI of individual twins			
TFEQ	β [95% CI]	p-value	n
Cognitive restraint	0.1 [-0.7, 0.8]	0.85	176
Disinhibited eating	1.7 [1.0, 2.5]	<0.001	176
Hunger susceptibility	0.1 [-0.7, 0.9]	0.78	176
DEBQ			
Restrained eating	1.3 [0.6, 2.0]	<0.001	245
External eating	0.2 [-0.4, 0.9]	0.50	248
Emotional eating	0.6 [-0.04, 1.3]	0.07	247
BES			
Binge-eating score	1.8 [1.2, 2.5]	<0.001	268
EDI-2			
Drive for thinness	1.5 [-0.7, 2.3]	<0.001	255
Body dissatisfaction	3.2 [2.5, 3.9]	<0.001	255
Bulimia	0.9 [0.2, 1.5]	0.01	258

310 n=number of individuals, BMI=body mass index, TFEQ=Three Factor Eating Questionnaire,
311 DEBQ=Dutch Eating Behaviour Questionnaire, BES=Binge-eating Scale, EDI-2=Eating Disorder
312 Inventory-2, β [95% CI]=regression coefficient with 95% confidence interval from survey regressions.

313
314 In BMI-discordant MZ and DZ twin pairs, evidence was present for higher disinhibited
315 eating (TFEQ), binge-eating scores (BES; $p=0.050$ in MZ pairs), and body
316 dissatisfaction (EDI-2) in the heavier co-twins (Figure 2). Only in DZ twins did the
317 heavier co-twins show higher restrained eating (DEBQ), and drive for thinness (EDI-

2). No important intra-pair differences appeared in the BMI-concordant groups (Supplementary Figure S2).

The common language effect size for disinhibited eating in MZ BMI-discordant twin pairs was 0.74 [0.57, 0.95] (effect size [95% CI]) and in DZ twin pairs 0.76 [0.62, 0.94]. The effect size for binge-eating score in MZ twin pairs was 0.71 [0.50, 1.001] and in DZ twin pairs 0.73 [0.58, 0.92], and for body dissatisfaction in MZ twin pairs this was 0.73 [0.54, 0.99] and in DZ pairs 0.81 [0.72, 0.91].

In DZ BMI-discordant female twins, the intra-pair differences in body dissatisfaction and bulimia were significantly larger than in male twins, which were the only sex-differences among all groups (Supplementary Table S6).

The behavioural traits had mostly negligible and low intercorrelations (although p-values showed evidence of associations between traits), aside from three moderate correlation coefficients (Supplementary Table S7).

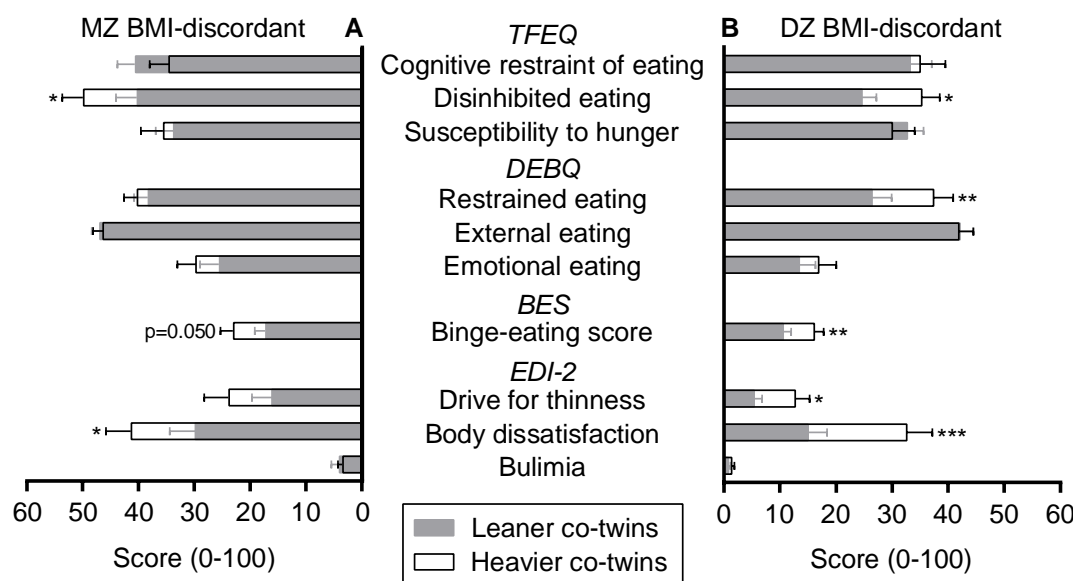


Figure 2: Overlay bar graph with mean±standard error scores on eating behavioural traits in leaner and heavier (panel A) monozygotic (MZ) and (panel B) dizygotic (DZ) co-twins in pairs discordant for body mass index (BMI). TFEQ=Three Factor Eating Questionnaire, DEBQ=Dutch Eating Behaviour Questionnaire, BES=Binge-eating Scale, EDI-2=Eating Disorder Inventory-2. Wilcoxon signed-rank test *p<0.05, **p<0.01, ***p<0.001.

After further division of the TFEQ outcome measures into seven subscales (Figure 3), the leaner co-twins of the MZ BMI-discordant twin pairs showed significantly higher flexible control. The effect size for flexible control was 0.28 [0.08, 0.95]. The heavier co-twins of this group demonstrated particularly stronger habitual disinhibition (Figure 3), for which the effect size was 0.78 [0.65, 0.93]. No significant differences were present in the DZ BMI-discordant twin pairs. In BMI-concordant MZ twin pairs, a stronger flexible control of the leaner co-twins was found (Supplementary Figure S3), with an effect size of 0.21 [0.04, 0.99].

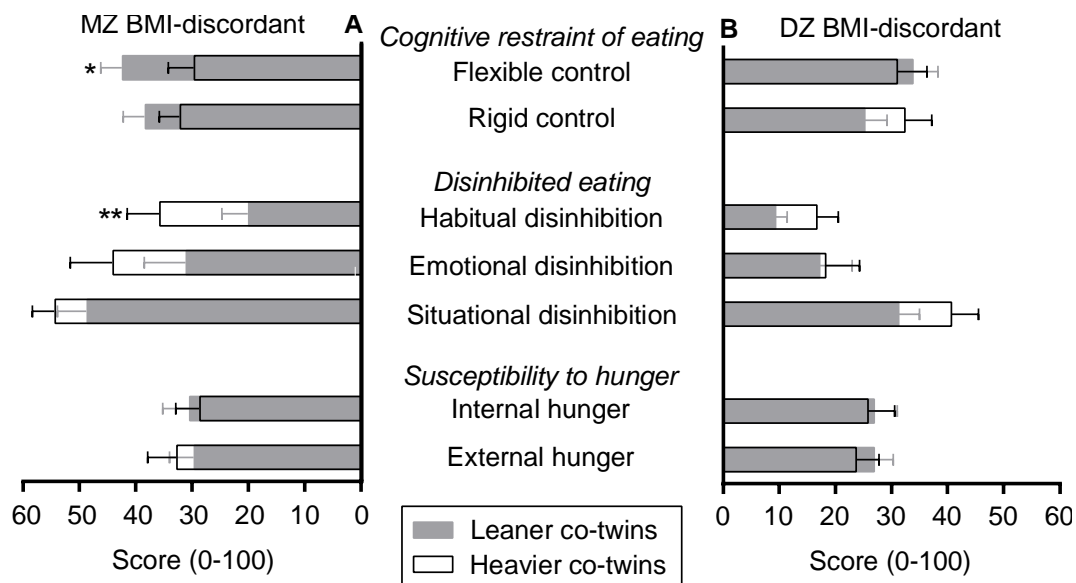


Figure 3: Overlay bar graph with mean±standard error scores on subscales of the Three Factor Eating Questionnaire in leaner and heavier (panel A) monozygotic (MZ) and (panel B) dizygotic (DZ) co-twins in pairs who are discordant for body mass index (BMI). Wilcoxon signed-rank test * $p < 0.05$, ** $p < 0.01$.

3.4 Leaner and heavier co-twins' judgment of each others' eating behaviours

In the co-twin comparison questionnaire, the twins rated their own eating behaviours in comparison to their co-twin's eating behaviours (Figure 4), for example, "which of you (you or your co-twin) eats more?" (Supplementary Text S2). In panel A of Figure 4, the BMIs of only those twin pairs who gave the same, internally consistent response on which co-twin performs the behaviour more strongly were compared with the Wilcoxon signed-rank test. The number of twin pairs who agreed on which of them performed a behavioural trait varied per trait (ranging from 10 to 26 out of 55 MZ and from 13 to 27 out of 65 DZ twin pairs). The strongest significant effects on BMI were for the MZ twins who ate more food (+5.2 kg/m²), and more fatty food (+4.4 kg/m²), snacks (+4.0 kg/m²), and healthy food (-4.7 kg/m²), and were more worried about their appearance (-5.2 kg/m²), as well as smaller but significant findings for eating more sweet and fatty delicacies (+2.3 kg/m²), eating more regularly (-2.6

364 kg/m²), and more slowly (-2.3 kg/m²). In the DZ twins, significant associations with
365 BMI were for eating more food (+4.9 kg/m²), fatty food (+3.5 kg/m²), and snacks (+3.6
366 kg/m²).

367 In panel B of Figure 4, all twin pairs were included for multivariate regression
368 analyses adjusted for age and sex. Intra-pair comparisons of several eating
369 behavioural traits were associated with BMI differences. Eating more food and more
370 fatty food were linked to an intra-pair difference in BMI of +2.3 and +2.4 kg/m² in MZ
371 twins, and +2.3 and +2.6 kg/m² in DZ twins. Furthermore, in MZ twins, eating more
372 snacks was linked to a BMI difference of +1.8 kg/m², whereas eating more healthy
373 food and eating more regularly, as well as being more worried about one's
374 appearance were associated with negative BMI differences (-2.4, -1.8 and -2.7
375 kg/m²).

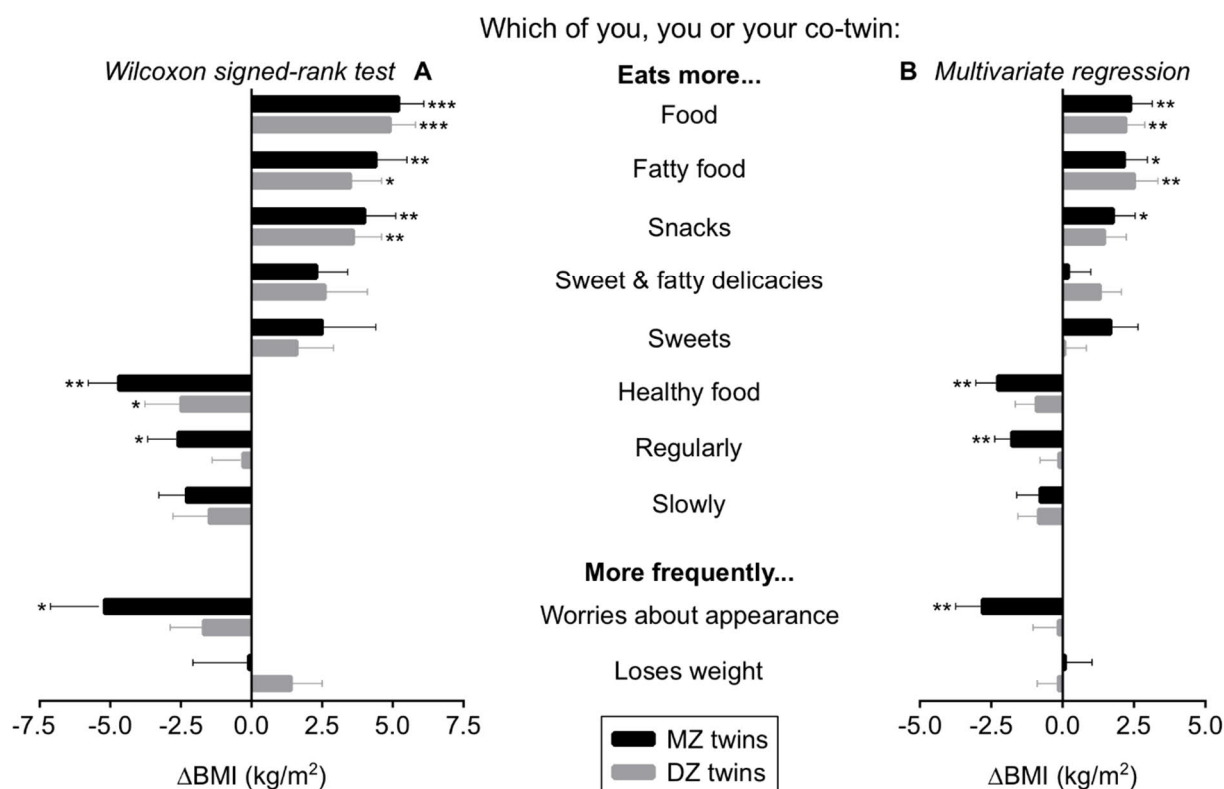


Figure 4: (panel A) Wilcoxon signed-rank test was used to compare body mass index (BMI) within monozygotic (MZ) and dizygotic (DZ) twin pairs who gave an internally consistent answer; (panel B) Multivariate regression analyses were performed within all twin pairs, and indicated the association ($\beta \pm$ standard error) between co-twin differences in eating behaviours and intra-pair differences in BMI (Δ BMI) in kg/m^2 , controlled for age and sex. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

4. Discussion

In both MZ and DZ BMI-discordant twin pairs, the heavier co-twins reported difficulties regulating their food intake optimally, and they also reported overall unhealthier eating behavioural traits than did their leaner counterparts. Both twins in such pairs more frequently agreed that the heavier co-twins ate more food and fatty food than did their leaner co-twins, and that in MZ twins the heavier co-twins exhibited an overall unhealthier eating pattern. In BMI-concordant twin pairs, the leaner and heavier co-twins had comparable eating behaviour. The discussion will focus on BMI-discordant twin pairs, unless stated otherwise.

Initially, we inquired whether the twins were capable of consuming an appropriate amount of food within the twins' perceived requirements. The majority of the heavier MZ and DZ co-twins reported being less capable of eating according to their needs. Instead, they characterized their primary behaviour as frequent overeating, in line with our previous findings (Pietiläinen et al., 2010). Notably, in the current study more than half of the leaner MZ co-twins self-reported non-optimal eating. The reason may be that even the leaner MZ co-twins experienced on average overweight, and perhaps therefore displayed healthier behavioural traits. Another preceding investigation of this question demonstrated that both restrictive and overeating behaviours increased the risk for obesity (A. Keski-Rahkonen et al., 2007). Overall, studies in naturalistic settings confirm the common co-occurrence of overeating and restraint, but primarily support the beneficial effects of restraint in reducing overeating and promoting weight loss (Johnson, Pratt, & Wardle, 2012; Schaumberg et al., 2016). The current findings also support the association of overeating, rather than food restriction, with a higher BMI, independent of genotype and shared environment.

Augmented disinhibited eating (TFEQ) and binge-eating scores (BES) in the heavier MZ and DZ co-twins further revealed the association between overeating and increased BMI. Disinhibited eating has been linked to BMI (Bryant et al., 2007), and the current study adds evidence for this association independent of genetic and shared environmental factors. Important to note is that the mean value of the binge-eating score implies that the participants are non-bingers. This was in accordance with our exclusion of those with eating disorders. A non-binger might still overeat, but without a dysphoric response (Gormally et al., 1982).

Disinhibited eating was divided into habitual, situational and emotional disinhibition subscales (Bond et al., 2001). These provide more detailed information on the nature of disinhibited eating, which may facilitate the tailoring of interventions. Of all seven TFEQ subscales, habitual disinhibition has most strongly predicted weight gain over 20 years (Hays & Roberts, 2008). For us, the heavier co-twins of the BMI-discordant MZ but not DZ twin pairs showed higher habitual disinhibition. Since this finding was not consistent for both zygositys, no inferences on genetic influence are possible.

We also investigated two restrictive eating behaviours; restrained eating (DEBQ) and cognitive restraint of eating (TFEQ). Both mainly target restrictions from desired, rather than required, ingestion of food (Lowe & Levine, 2005; van Strien, 2008). Hence, high scores on these restraint measures are no guarantee that individuals are restricting their food intake appropriately to lose weight. Furthermore, restrained eating (DEBQ) measures an intention to restrict food intake, whereas cognitive restraint of eating (TFEQ) measures actual caloric restraint (Williamson et al., 2007). We found restrained eating (DEBQ) to characterize the heavier rather than the leaner co-twins of the DZ twin pairs. However, the cognitive restraint of eating (TFEQ) did not differ within the pairs with either of the zygositys. This suggests that the heavier DZ co-twins here had the intention to restrict, but did not actually restrict food intake. Therefore, they might have intended to incorporate restrained eating as a compensatory mechanism for overeating. We cannot, however, exclude the possibility that restrained eating initiated disinhibited eating for those individuals with high scores on both scales (Ouwens, van Strien, & van der Staak, 2003).

We divided cognitive restraint of eating (TFEQ) into two subscales; flexible control and rigid control of eating behaviour. Flexible control is a more gradual and

subtle approach to limiting food intake than is the all-or-nothing approach of rigid control (Westenhoefer, 1991). Rigid control methods include strict consumption rules, which, when broken, may initiate a loss of control of eating (disinhibited eating). Flexible control is known to be linked with decreased eating behaviour disturbances, decreased body weight, and increased success in weight loss and maintenance, as opposed to the negative health consequences of rigid control (Westenhoefer, Stunkard, & Pudel, 1999). Our findings support the view that flexible control may contribute to the BMI difference, at least within the MZ twin pairs. Flexible control was augmented in the leaner co-twins of the BMI-discordant and -concordant MZ twin pairs, even though the overarching cognitive restraint did not differ within the pairs.

The heavier co-twins reported higher body dissatisfaction (in both MZ and DZ pairs), and a stronger drive for thinness (in DZ pairs). Both traits have previously been associated with larger body size (Anna Keski-Rahkonen et al., 2005), and we can complement this with our finding that body dissatisfaction was associated with BMI independent of genotype and shared environment. The intra-pair differences on the EDI-2 questionnaire were significantly larger for DZ females than for males. This was expected, because body dissatisfaction in those who have obesity compared to normal-weight individuals has been recognized to be considerably higher in women than in men (Weinberger et al., 2016).

The co-twin comparison questionnaire included both BMI-discordant and concordant twin pairs, and asked all twins to compare their own behaviour with their co-twin's behaviour, as in previous studies (Bogl et al., 2009; Pietiläinen et al., 2010; Rissanen et al., 2002). This approach is advantageous because it provides a verification of behavioural traits by the co-twins, who are reliable proxies of each other's behaviours (Hamilton & Mack, 2000). In our study, the percentage of

agreement, within pairs on which co-twin performs which behaviour more strongly is relatively low, this may be because only 2 out of 16 possible answer combinations defined an agreement in the direction of either co-twin. Within the disagreement proportion the answers were diluted over the remaining fourteen answer combinations. Regardless, both MZ and DZ twin pairs agreed more frequently that the heavier co-twin ate more food in general, and more fatty food in particular than their leaner counterparts, in comparison to a vice versa agreement. Additionally, in MZ twins, eating more snacks was associated with a higher BMI, while eating more healthy food, having a regular eating pattern, and being concerned about one's appearance were linked with a lower BMI. Similar behaviours have been associated with BMI in MZ (Bogl et al., 2009; Pietiläinen et al., 2010; Rissanen et al., 2002) and DZ (Bogl et al., 2009) twin pairs. In these studies, no link emerged between eating regularly and BMI, except one reported an association of obesity with a higher intake of sweet and fatty delicacies (Bogl et al., 2009). None of these studies, including ours, found clear differences in BMI based on sweet consumption. Evidence on the associations between sugar intake and body weight remains inconsistent (van Baak & Astrup, 2009).

In the food diaries, the leaner and heavier co-twins of the BMI-discordant pairs reported similar dietary intakes, approximately in line with the Nordic Nutrition Recommendations (Nordic Council of Ministers, 2014). However, it is likely that the heavier co-twins significantly underreported, as shown with the doubly labelled water method in our previous sample of BMI-discordant MZ twin pairs (Pietiläinen et al., 2010). Furthermore, undereating during dietary recording periods is a common reason for dietary misreporting, especially by those experiencing obesity (Goris et al., 2000).

491 The current study did not consider energy expenditure, achieved largely
492 through physical activity (PA). In our earlier study, one on PA and metabolic
493 outcomes, we investigated approximately 25 of the same MZ BMI-discordant twin
494 pairs included here (Berntzen et al., 2018). The heavier co-twins took on average
495 nearly 2000 fewer steps per day, and performed approximately 15 minutes less
496 moderate to vigorous PA. Therefore, the PA deficiency in the heavier co-twins likely
497 contributes to the presence of BMI-discordance in these twin pairs. This may also
498 partly explain the lower than expected caloric intake of the heavier co-twins.

499 The current study suggests that a direct question addressing the subjective
500 ability to regulate food intake may be more reliable in screening obesity-related
501 eating patterns in young adults than are food diaries. Additionally, the disinhibited
502 eating measure (TFEQ) might serve as a comprehensive observational tool to
503 capture relevant motives for overeating. Future research should explore the suitability
504 of the food intake regulation question and the disinhibited eating measure for
505 screening and diagnostic purposes, complemented by intervention studies on these
506 behaviours. For example, incorporating a new healthy habit in daily life may diminish
507 habitual disinhibition (Lillis et al., 2016; Rock et al., 2017). Another focus could be on
508 flexible control of eating behaviour, as this was found to diminish the effect of
509 habitual disinhibition on BMI (Hays & Roberts, 2008). Besides this, upcoming studies
510 should try to implement surveys similar to the co-twin comparison questionnaire in
511 populations other than twins; for example through inclusion of individuals who can
512 serve as reliable proxy informants for the eating behaviour of the participants (e.g.,
513 spouse, sibling, other relative, or close friend).

514 This study has strengths and limitations. The design was cross-sectional, so
515 no inferences can be made on causality between eating behaviour and BMI.

516 Information on their socio-economic status was unavailable and was therefore absent
517 as a potential confounder in the models. In general, however, twin pairs have a high
518 concordance for educational attainment and socio-economic status (Marks, 2017;
519 Silventoinen, Kaprio, & Lahelma, 2000). The co-twin control design is unique, but due
520 to the rarity of BMI-discordant pairs the sample size was small (providing low
521 statistical power). Earlier reports on similar eating behaviours in twins who vary in
522 BMI exist, however with even smaller sample sizes (Pietiläinen et al., 2010; Rissanen
523 et al., 2002). We applied more lenient inclusion criteria to reach a larger sample size.
524 Instead of a difference in an internationally defined cut-off point of BMI (e.g. healthy
525 weight vs. obesity), we considered now any minimum of a 3-point difference in BMI
526 important (averaging about 10 kg difference in a person with a height of 170 cm). For
527 example, within the healthy weight category, a BMI of 24 versus a BMI of 20
528 increases risk for type II diabetes (Lehtovirta et al., 2010). Beyond the slightly
529 increased sample size, our study investigated for the first time in such a twin design
530 (to our knowledge) the DEBQ, the comprehensive version of the TFEQ, and the
531 subtypes of behavioural traits from the TFEQ. None of the questionnaires in our
532 study were previously studied in DZ BMI-discordant twin pairs, except the co-twin
533 comparison questionnaire (Bogl. et al 2009). Differences in anthropometry appeared
534 between MZ and DZ twins, possibly explained by a genetic pressure for similarity in
535 MZ pairs. Consequently, discordance in weight is more likely to occur at higher age in
536 MZ pairs. Higher age in itself links with weight gain, which may explain the mild
537 overweight in the leaner co-twins of MZ but not DZ pairs. We performed many tests
538 and reported nominal p-values of the differences with conservative non-parametric
539 tests (Sullivan & Artino, 2013). Perhaps, a multiple testing correction could have been
540 applied. However, we tested behavioural traits only by BMI-discordance, so no

exhaustive associations between behaviours and potentially irrelevant outcome measures were performed to force an appearance of low p-values. A multiple testing correction would be overly conservative and could promote type II errors in a small cohort.

We included several validated and reliable questionnaires, and were thus able to examine a multitude of eating behavioural aspects within the same research population. This established a robust and comprehensive overview of variations in eating behavioural dimensions associated with BMI-discordance, regardless of numerous personal (age, sex, genes etc.) and shared environmental (*in utero*, childhood, socio-economic, neighbourhood environment) factors.

5. Conclusions

Overeating – measured by “frequent overeating”, “disinhibited eating”, and “binge-eating score” – emerged as the main behaviour associated with higher BMI. The twins agreed more frequently that their heavier co-twins habitually ate more food, and particularly more fatty food. Furthermore, the heavier co-twins were generally less satisfied with their bodies. These findings were independent of genetic and shared environmental influences.

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8. Conflict of Interest

None

9. Ethical approval

The authors assert that all procedures contributing to this work comply with the ethical standards of the relevant national and institutional committees on human experimentation and with the Helsinki Declaration of 1975, as revised in 2008.

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762 **11. Supplementary material**

763 Supplementary Text S1: Food intake regulation question.

764 Which of the following four alternatives best describes you?

765 1. It is easy for me to eat about the amount I need to → Optimal eating

766 2. I quite often eat more than I actually need → Frequent overeating

767 3. I often try to restrict my eating → Frequent restricted eating

768 4. At times, I'm on a strict diet, at others I overeat → Alternating overeating and restriction

769 Supplementary Text S2: Co-twin comparison questionnaire.
770 Which of you (you or your co-twin), ...
771 – Eats more?
772 – Eats more snacks?
773 – Eats more fatty foods?
774 – Eats more sweet & fatty delicacies (chocolate, pastries, ice cream)?
775 – Eats more sweets (candies or jellies)?
776 – Selects food more according to healthiness?
777 – Eats more regularly?
778 – Eats more slowly?
779 – Is more worried about appearance?
780 – Goes on diets more often?
781 Response alternatives: Me, My co-twin, There is no difference between us, Do not know.

782 Supplementary Table S1: Number of twin pairs for whom data is available for the eating behavior
783 questionnaires.

	BMI-discordant twin pairs		BMI-concordant twin pairs	
	MZ (n=29)	DZ (n=46)	MZ (n=28)	DZ (n=31)
Anthropometry	29	46	28	31
TFEQ				
Cognitive restraint	28	31	15	15
Disinhibited eating	28	31	14	15
Hunger susceptibility	28	31	14	15
DEBQ				
Restrained eating	28	35	28	30
External eating	29	36	28	31
Emotional eating	29	36	28	30
BES				
Binge-eating score	29	46	28	31
EDI				
Drive for thinness	26	40	24	31
Body dissatisfaction	25	44	26	29
Bulimia	26	40	25	30
Food diary	28	35	28	30
Food intake regulation	29	36	24	30
Co-twin comparison	29	35	26	30

784 BMI=body mass index, MZ=monozygotic, DZ=dizygotic, n=total available number of pairs, TFEQ=Three
785 Factor Eating Questionnaire, DEBQ=Dutch Eating Behavior Questionnaire, BES=Binge-Eating Scale, EDI-
786 2=Eating Disorder Inventory-2.

787 Supplementary Table S2: Intra-pair differences in characteristics of MZ and DZ twin pairs concordant for BMI.

BMI-concordant twin pairs

	MZ (n=28)				DZ (n=31)			
	Leaner	Heavier	Δ%	p-value	Leaner	Heavier	Δ%	p-value
Age, y	30.3±0.5	30.3±0.5	-	-	28.3±0.4	28.4±0.4	-	-
Female/male, freq.	11/17	11/17	-	-	14/17	14/17	-	-
Height, cm	173.0±1.9	173.5±1.9	0.3	0.26	173.4±1.7	171.8±1.5	-0.9	0.23
Weight, kg	73.7±2.5	77.7±2.5	5.4	<0.001	71.0±2.6	74.6±2.7	5.1	0.002
BMI, kg/m ²	24.5±0.6	25.7±0.6	4.9	<0.001	23.5±0.6	25.2±0.7	7.2	<0.001
Fat mass, kg	19.9±1.4	22.7±1.5	14.1	<0.001*	19.7±1.3	21.6±1.5	9.6	0.02
Body fat, %	26.7±1.7	28.9±1.6	8.2	0.001*	27.4±1.6	28.6±1.7	4.4	0.16

788 Values are mean±standard error. BMI=body mass index, MZ=monozygotic, n=number of pairs, DZ=dizygotic,
789 Δ%=difference in percentages [(heavier-leaner)/leaner×100], freq.=frequency, *n=27 pairs.

790 Supplementary Table S3: Frequencies of BMI category comparisons within twin pairs.

All twin pairs						
	Underweight	Healthy weight	Overweight	Obesity class I	Obesity class II	Obesity class III
Underweight	1	2	3	1		
Healthy weight		39	37	10	2	
Overweight			14	12	5	1
Obesity class I				2	3	
Obesity class II						1
Obesity class III						1

BMI-discordant pairs						
	Underweight	Healthy weight	Overweight	Obesity class I	Obesity class II	Obesity class III
Underweight			3	1		
Healthy weight		9	31	10	2	
Overweight			1	8	5	1
Obesity class I					2	
Obesity class II						1
Obesity class III						1

MZ BMI-discordant pairs						
	Underweight	Healthy weight	Overweight	Obesity class I	Obesity class II	Obesity class III
Underweight						
Healthy weight		1	11	3		
Overweight			1	6	2	1
Obesity class I					2	
Obesity class II						1
Obesity class III						1

791 BMI=body mass index (kg/m^2), MZ=monozygotic, DZ=dizygotic, underweight: $\text{BMI} < 18.5$; healthy weight: $18.5 \leq \text{BMI} < 25$; overweight: $25 \leq \text{BMI} < 30$; obesity
792 class I: $30 \leq \text{BMI} < 35$; obesity class II: $35 \leq \text{BMI} < 40$; obesity class III: $\text{BMI} \geq 40$.

793 Supplementary Table S3 (continued): Frequencies of BMI category comparisons within twin pairs.

DZ BMI-discordant pairs						
	Underweight	Healthy weight	Overweight	Obesity class I	Obesity class II	Obesity class III
Underweight			3	1		
Healthy weight		8	20	7	2	
Overweight				2	3	
Obesity class I						
Obesity class II						
Obesity class III						

BMI-concordant pairs						
	Underweight	Healthy weight	Overweight	Obesity class I	Obesity class II	Obesity class III
Underweight	1	2				
Healthy weight		30	6			
Overweight			13	4		
Obesity class I				2	1	
Obesity class II						
Obesity class III						

MZ BMI-concordant pairs						
	Underweight	Healthy weight	Overweight	Obesity class I	Obesity class II	Obesity class III
Underweight		1				
Healthy weight		13	4			
Overweight			8	1		
Obesity class I					1	
Obesity class II						
Obesity class III						

794 BMI=body mass index (kg/m²), MZ=monozygotic, DZ=dizygotic, underweight: BMI<18.5; healthy weight: 18.5≤BMI<25; overweight: 25≤BMI<30; obesity
795 class I: 30≤BMI<35; obesity class II: 35≤BMI<40; obesity class III: BMI≥40.

796 Supplementary Table S3 (continued): Frequencies of BMI category comparisons within twin pairs.

DZ BMI-concordant pairs						
	Underweight	Healthy weight	Overweight	Obesity class I	Obesity class II	Obesity class III
Underweight	1	1				
Healthy weight		17	2			
Overweight			5	3		
Obesity class I				2		
Obesity class II						
Obesity class III						

797 BMI=body mass index (kg/m²), MZ=monozygotic, DZ=dizygotic, underweight: BMI<18.5; healthy weight: 18.5≤BMI<25; overweight: 25≤BMI<30; obesity

798 class I: 30≤BMI<35; obesity class II: 35≤BMI<40; obesity class III: BMI≥40.

799 Supplementary Table S4: P-values, from an independent samples Mann-Whitney U test for continuous
800 variables and the Fisher’s exact test for categorical variables, of monozygotic versus dizygotic co-twins
801 (leaner vs. leaner, and heavier vs. heavier) separately for co-twins from body mass index discordant and
802 concordant pairs.
803

	BMI-discordant		BMI-concordant	
	Leaner MZ vs. DZ	Heavier MZ vs. DZ	Leaner MZ vs. DZ	Heavier MZ vs. DZ
	co-twins	co-twins	co-twins	co-twins
Age, y	0.03	0.04	0.02	0.02
Female/male, freq.	0.10	0.10	0.79	0.79
Height, cm	0.73	0.37	0.96	0.43
Weight, kg	0.005	0.19	0.34	0.20
BMI, kg/m ²	<0.001	0.02	0.17	0.41
Fat mass, kg	<0.001	0.007	0.76	0.56
Body fat, %	<0.001	0.01	0.56	0.87

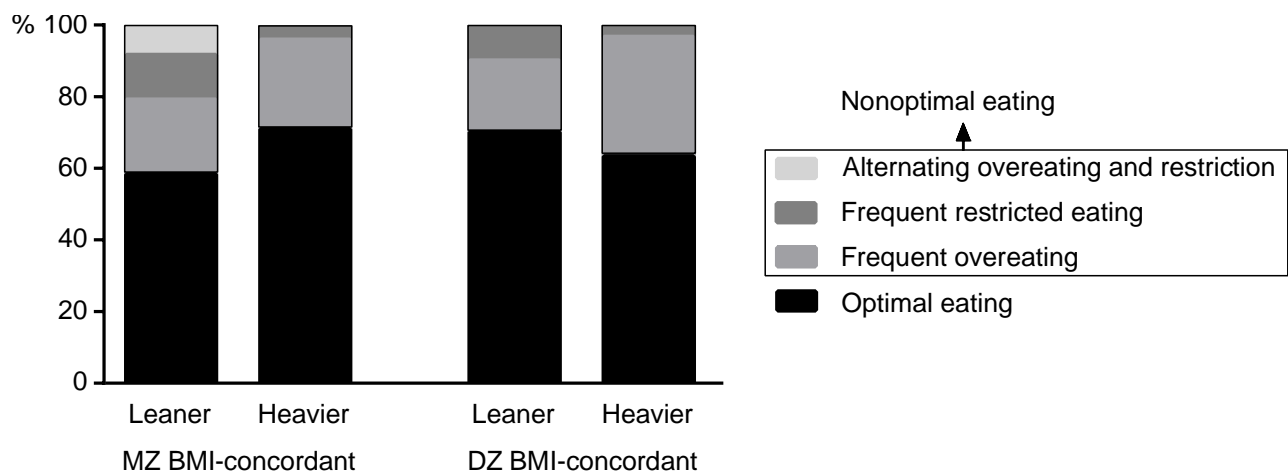
804 BMI=body mass index, MZ=monozygotic, DZ=dizygotic.
805

806 Supplementary Table S5: Dietary components in BMI-discordant and -concordant MZ and DZ twins.

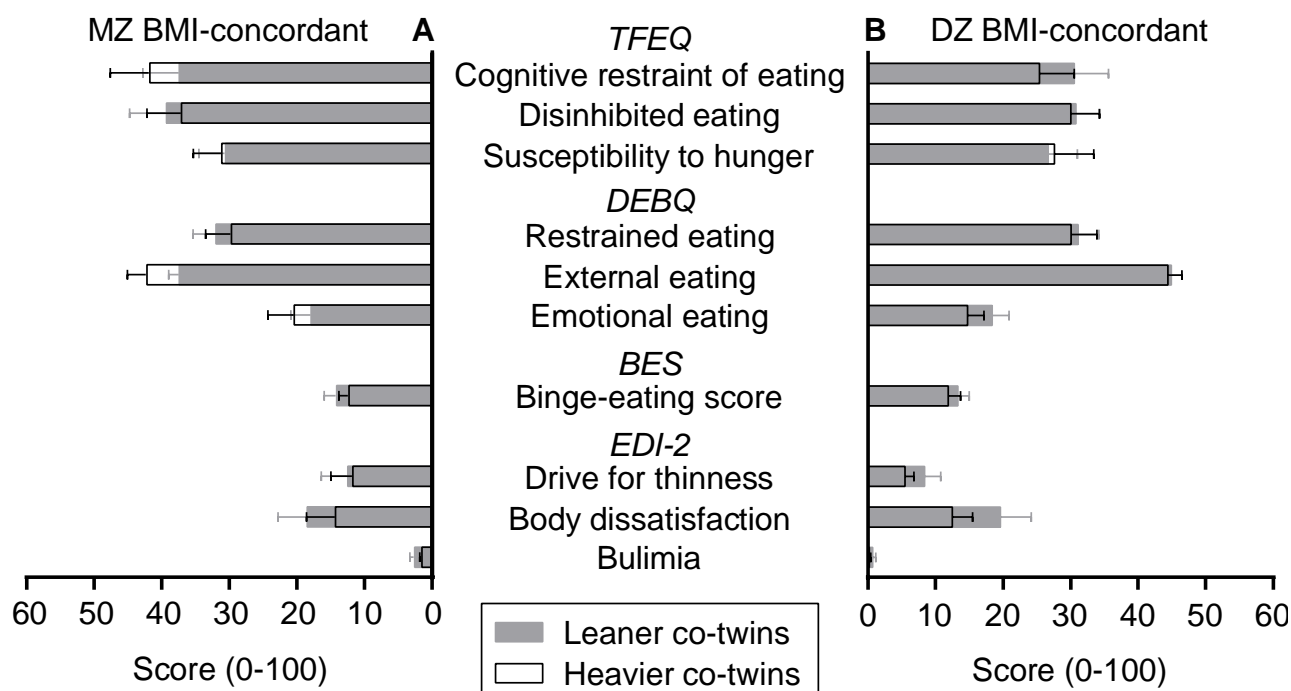
BMI-discordant twin pairs						
	MZ (n=28)		<i>P</i> -value	DZ (n=30)		<i>p</i> -value
	Leaner	Heavier		Leaner	Heavier	
Total calories, kcal/d	2008±104	2082±115	0.96	2046±91	2201±121	0.31
Carbohydrate, g/d	218.6±11.9	219.1±14.0	0.91	240.0±11.9	266.3±19.4	0.40
Carbohydrate, % energy	43.9±1.3	42.4±1.6	0.18	47.2±1.4	47.5±1.3	0.87
Sugar, g/d	101.4±8.2	103.5±11.8	0.63	100.5±6.5	103.8±8.6	0.90
Sucrose, g/d	51.0±6.0	53.5±9.3	0.80	52.9±5.1	47.9±4.3	0.44
Fructose, g/d	12.6±1.8	14.6±2.0	0.41	11.9±1.3	16.8±2.4	0.28
Protein, g/d	89.7±7.2	89.1±5.8	0.96	88.0±4.4	90.8±5.3	0.73
Protein, % energy	17.8±0.9	17.3±0.6	0.89	17.2±0.5	16.8±0.7	0.68
Fat, g/d	81.1±5.8	84.7±5.2	0.82	78.4±5.5	79.5±4.5	0.62
Fat, % energy	35.7±1.3	36.6±1.3	0.73	33.8±1.4	32.5±1.1	0.53
Saturated fats, g/d	32.6±2.6	31.2±2.1	0.32	30.1±2.4	28.9±1.6	0.96
Alcohol, g/d	7.6±2.2	13.7±3.9	0.53	5.1±1.4	9.5±2.4	0.21
Alcohol, % energy	2.7±1.0	3.8±1.0	0.63	1.8±0.5	3.2±0.8	0.23
Dietary fiber, g/d	17.9±1.7	17.4±1.2	0.84	19.1±1.3	21.9±1.9	0.38

BMI-concordant twin pairs						
	MZ (n=28)		<i>P</i> -value	DZ (n=31)		<i>p</i> -value
	Leaner	Heavier		Leaner	Heavier	
Total calories, kcal/d	1950±94	2158±101	0.12	2014±108	2279±184	0.50
Carbohydrate, g/d	228.6±13.4	243.0±12.9	0.23	242.9±15.3	272.6±23.3	0.56
Carbohydrate, % energy	46.7±1.6	45.0±1.5	0.23	48.2±1.5	48.0±1.3	0.67
Sugar, g/d	101.9±8.5	97.9±7.6	0.66	100.6±6.9	113.9±9.0	0.31
Sucrose, g/d	53.5±5.5	49.0±4.7	0.49	47.4±5.0	59.2±5.5	0.18
Fructose, g/d	13.4±1.6	11.4±1.3	0.09	13.4±1.6	15.2±2.0	0.53
Protein, g/d	88.3±6.2	96.9±5.1	0.08	84.6±5.1	97.5±12.6	0.83
Protein, % energy	18.0±1.0	18.4±0.9	0.70	17.0±0.7	16.5±0.7	0.36
Fat, g/d	73.3±4.4	81.9±5.0	0.14	72.1±5.0	79.3±6.0	0.39
Fat, % energy	33.5±1.2	33.9±1.5	10.0	31.9±1.2	31.5±1.0	0.67
Saturated fats, g/d	29.6±2.0	29.7±1.9	0.98	26.1±1.9	30.9±2.6	0.08
Alcohol, g/d	4.3±1.8	10.1±4.3	0.59	9.0±2.0	13.3±3.3	0.45
Alcohol, % energy	1.7±0.7	2.7±1.1	0.66	2.9±0.6	4.0±1.0	0.48
Dietary fiber, g/d	18.7±2.0	18.2±1.7	0.95	18.4±1.5	17.9±1.8	0.34

807 Values are mean±standard error. MZ=monozygotic, BMI=body mass index, n=number of pairs, DZ=dizygotic,
808 kcal/d=kilocalories per day, g/d=grams per day, % energy=percentage of total energy intake.



809 MZ BMI-concordant DZ BMI-concordant
 810 Supplementary Figure S1: Percentages of food intake regulation categories in leaner and heavier
 811 monozygotic (MZ) and dizygotic (DZ) twins concordant for body mass index (BMI).



Supplementary Figure S2: Overlay bar graph with mean \pm standard error scores on eating behavioral traits in leaner and heavier (panel A) monozygotic (MZ) and (panel B) dizygotic (DZ) co-twins in pairs concordant for body mass index (BMI). TFEQ=Three Factor Eating Questionnaire, DEBQ=Dutch Eating Behavior Questionnaire, BES=Binge-eating Scale, EDI-2=Eating Disorder Inventory-2.

817 Supplementary Table S6: Intra-pair differences of characteristics and behavioral traits between MZ and DZ
818 BMI-discordant and -concordant male and female twin pairs.

	MZ BMI-discordant twin pairs			DZ BMI-discordant twin pairs		
	Male (n=10)	Female (n=19)	p-value	Male (n=25)	Female (n=21)	p-value
BMI, kg/m ²	5.7±0.7	6.2±0.7	0.82	6.6±0.7	7.9±0.7	0.08
Fat mass, kg	12.7±2.0	14.2±1.4	0.61	14.8±1.8	18.0±1.9	0.21
Body fat, %	8.2±2.3	9.5±1.1	0.55	12.3±1.7	13.6±1.6	0.87
TFEQ						
Cognitive restraint	-7.1±5.5	-5.3±6.3	0.79	7.8±5.0	-5.4±7.6	0.47
Disinhibited eating	4.4±4.6	12.5±6.8	0.30	5.9±4.7	16.5±5.5	0.24
Hunger susceptibility	1.4±6.0	2.0±6.6	0.55	-3.8±7.6	-1.5±6.7	0.45
DEBQ						
Restrained eating	4.3±4.1	0.8±4.5	0.44	12.6±4.4	8.6±6.5	0.65
External eating	-2.8±3.5	0.5±2.8	0.43	-4.5±3.9	6.0±4.6	0.11
Emotional eating	-.2±7.8	6.6±5.8	0.96	-0.6±3.8	9.4±5.6	0.23
BES						
Binge-eating score	4.3±4.0	6.6±4.6	0.93	3.7±2.3	7.7±3.2	0.28
EDI-2						
Drive for thinness	3.6±3.6	9.5±7.2	0.34	4.2±2.8	12.2±5.8	0.08
Body dissatisfaction	14.6±7.0	9.6±7.0	0.77	8.5±3.5	31.3±8.5	0.01
Bulimia	0.6±1.1	-1.1±2.8	0.75	-0.6±0.6	2.3±1.0	0.02

	MZ BMI-concordant twin pairs			DZ BMI-concordant twin pairs		
	Male (n=17)	Female (n=11)	p-value	Male (n=17)	Female (n=14)	p-value
BMI, kg/m ²	1.1±0.1	1.5±0.3	0.17	1.9±0.2	1.4±0.2	0.09
Fat mass, kg	2.8±0.6	2.7±0.9	1.00	1.6±1.3	2.2±0.7	0.72
Body fat, %	2.2±0.5	2.1±1.4	0.58	.6±1.3	2.0±1.1	0.45
TFEQ						
Cognitive restraint	-11.6±8.4	8.6±8.2	0.12	7.4±7.2	-1.2±5.3	0.69
Disinhibited eating	4.2±8.2	-1.3±4.1	0.74	1.1±5.0	0±9.9	0.95
Hunger susceptibility	2.4±5.6	-5.7±5.2	0.26	1.3±6.9	-7.1±12.4	0.69
DEBQ						
Restrained eating	1.0±4.7	4.1±6.8	0.33	4.3±4.6	-3.3±7.6	0.36
External eating	-4.7±4.0	-5.±3.8	0.71	0±3.7	1.3±3.0	0.97
Emotional eating	1.9±3.7	-9.4±6.0	0.17	8.0±3.7	-1.9±6.0	0.16
BES						
Binge-eating score	3.3±2.1	-0.4±3.3	0.16	1.8±3.1	0.8±3.2	0.69
EDI-2						
Drive for thinness	-2.7±3.8	5.7±4.2	0.14	1.4±2.1	4.8±5.4	0.84
Body dissatisfaction	2.8±2.7	6.3±7.6	1.00	1.6±3.6	13.4±6.4	0.33
Bulimia	2.7±1.9	-1.4±1.6	0.18	-0.3±0.3	1.5±1.0	0.07

819 Values are mean±standard error. MZ=monozygotic, BMI=body mass index, n=number of pairs,
820 DZ=dizygotic, TFEQ=Three Factor Eating Questionnaire, DEBQ=Dutch Eating Behavior Questionnaire,
821 BES=Binge-eating Scale, EDI-2=Eating Disorder Inventory-2.

822 Supplementary Table S7: Correlation matrix of individual eating behavioral traits.

Survey		TFEQ			DEBQ			BES	EDI-2		
		Cognitive restraint	Disinhibited eating	Hunger susceptibility	Restrained eating	External eating	Emotional eating	Binge eating score	Drive for thinness	Body dissatisfaction	Bulimia
TFEQ	Cognitive restraint	1.00									
	Disinhibited eating	0.03*	1.00								
	Hunger susceptibility	0.0008	0.28***	1.00							
DEBQ	Restrained eating	0.53***	0.17***	0.007	1.00						
	External eating	0.02	0.26***	0.20***	0.19***	1.00					
	Emotional eating	0.03***	0.54***	0.15	0.16***	0.33***	1.00				
BES	Binge-eating score	0.03*	0.61***	0.22***	0.21***	0.28***	0.32***	1.00			
EDI-2	Drive for thinness	0.15***	0.29***	0.04*	0.26***	0.12***	0.18***	0.39***	1.00		
	Body dissatisfaction	0.05**	0.28***	0.01	0.22***	0.08***	0.16***	0.34***	0.38***	1.00	
	Bulimia	0.0001	0.33***	0.11***	0.02*	0.07***	0.18	0.31***	0.18**	0.11**	1.00

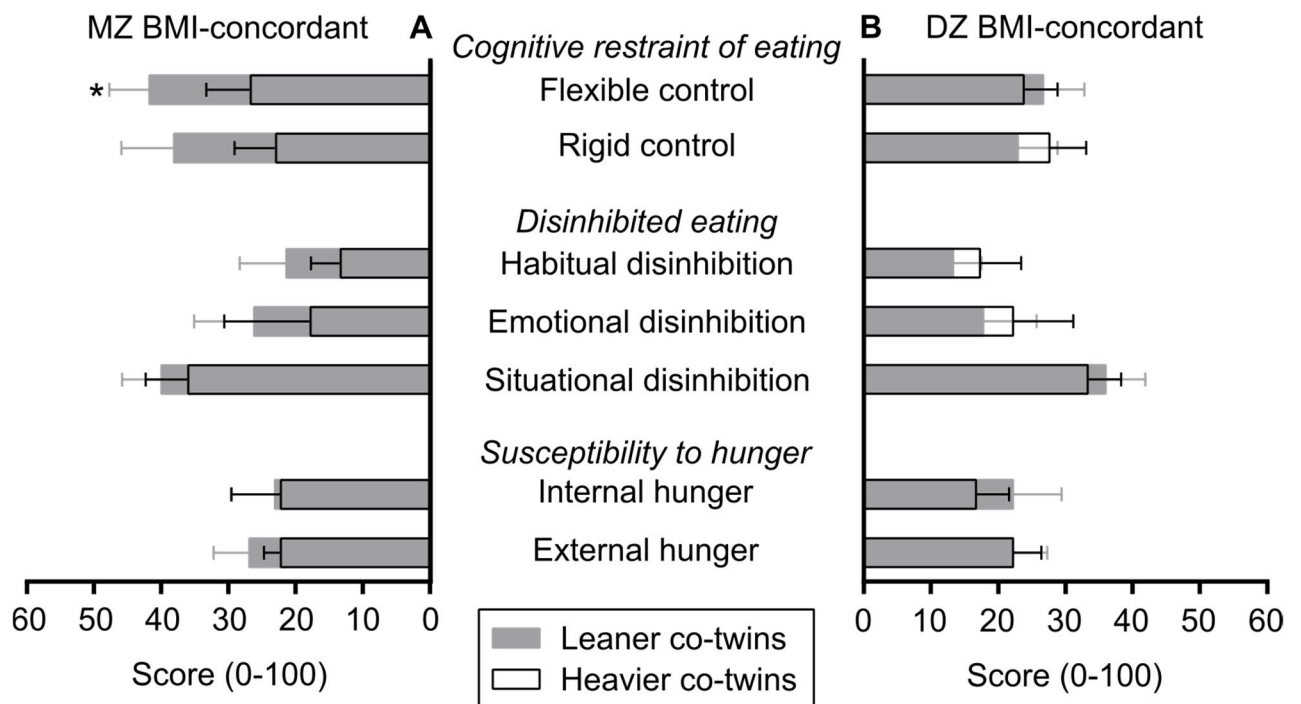
823 TFEQ: Three Factor Eating Questionnaire; DEBQ: Dutch Eating Behavior Questionnaire; BES: Binge-eating Scale; EDI-2: Eating Disorder Inventory-2.

824 Correlation coefficient size (Hinkle et al. 2003): negligible, $r=0.00-0.30$; low, $r=0.30-0.50$; moderate, $r=0.50-0.70$; high, $r=0.70-0.90$; very high, $r=0.90-1.00$.

825 * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

826 Reference: Hinkle DE, Wiersma W, Jurs SG (2003) Applied statistics for the behavioral sciences. Houghton Mifflin, Boston, Mass.; London

827



Supplementary Figure S3: Overlay bar graph with mean \pm standard error scores on subscales of the Three Factor Eating Questionnaire in leaner and heavier (panel A) monozygotic (MZ) and (panel B) dizygotic (DZ) co-twins in pairs who are concordant for body mass index (BMI). Wilcoxon signed-rank test * $p < 0.05$.